

NEW PRONOPHILINE BUTTERFLIES FROM THE VENEZUELAN TEPUYES
(NYMPHALIDAE: SATYRINAE)

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ABSTRACT. Four new species of satyrine butterflies collected in four Venezuelan tepuyes are described and illustrated: *Protopedaliodes ridouti* from the Roraima-Tepui, *Protopedaliodes profauna* and *Pedaliodes terramaris* from the Auyán-Tepui, and *Pedaliodes yutajeana* from the Cerros Yutajé, Yaví, and Marahuaka. Taxonomic considerations and discussion on affinities are presented.

Additional key words: Pantepui, *Pedaliodes*, Pleistocene, *Protopedaliodes*, Venezuela.

Venezuelan scientists involved in research on the tepuyes (most of them currently within national parks) have made major efforts to decrease and limit the so-called “ecological tourism” in this region. This is due mainly to their concern over the dramatic degradation of the fragile environments at the tops of these mountains. Propaganda recently generated by science fiction films (often recalling the imaginary Lost Worlds of Conan-Doyle and Crichton) and persons attempting to set new Guinness’ records in the tepuyes generate public clamor and still more visitor interest in the area. The accumulated result of such misguided publicity, together with the general paranoia about commercial collecting of wild animals and plants anywhere in the national territory, has resulted in the thoughtless enforcement of rigorous laws that virtually prohibit biological research in most of the Venezuelan protected areas.

Consequently, there is now an exceedingly complex bureaucracy to deal with in applying for insect collecting permits in the tepuyes (and elsewhere in Venezuela). Generally speaking, three separate applications must be prepared for the consideration and approval, respectively, of the National Council for Scientific and Technological Research (CONICIT), the National Parks Institute (INPARQUES), and finally the Service for the Fauna of the Ministry of Environment and Natural Resources (PROFAUNA). They have to be submitted synchronously and well in advance, taking into account the fact that the delivery of the third of these depends on the approval of the second, and so on. Even if these endless requirements were all satisfactorily met at the initial submission, we have found that there is no guarantee of receiving such permission, and when

given, permits are often so badly delayed that are out-of-date and useless.

To face this problem has become an essential worry for Venezuelan scientists (let alone foreigners), who find themselves handicapped in their field work, even if they are entirely innocent of any involvement with film and TV productions, or commercial dealing with biological specimens. As “illegal” procedures are being sternly punished with confiscation of material, financial penalties, and menace of imprisonment, it is rather frustrating to find that we are virtually forbidden to study our own biota while at the same time extensive gold mining (never controlled as are insect collecting activities) is quickly devastating large areas of pristine forests in marginal regions of the Venezuelan territory. These include all National Parks south of the Orinoco. Massive “ecotourism” and all its undesirable consequences however continues with no problems of permission (just a local application, approved on the day of submission) in the Canaima National Park and all of the tepuyes, even in the remotest Cerro de La Neblina.

This scenario leads us to believe that it will take several decades for Venezuelan and international scientists to be able to study good series of entomological samples from the tepuyes, which can satisfy the accepted paradigm of having two or more individuals to proceed to a satisfactory taxonomic description. In the meantime, we strongly feel that a few butterflies we know as undescribed, collected in four of the 54 tepuyes existing in Venezuela (all potentially populated by these insects), deserve to be described as part of a major revisionary work of the group currently being undertaken by the senior author. Two of these undescribed taxa are known from single male individuals. One is so distinctive within an endemic and hitherto monobasic genus (which was erected by ourselves in 1994) that we would not hesitate in providing a new place for it in the increasing list of Neotropical butter-

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fly names; the other one, although externally undistinguished, is also a new member of a small group of species which may be unmistakably recognized by the contortion of the tip of the male genitalic valvae.

Four descriptions are presented here. All type specimens, except for the solitary individual of *Protopedaliodes ridouti*, new species, which is held by The Natural History Museum (BMNH) in London, are deposited in the Museo del Instituto de Zoología Agrícola of the Universidad Central de Venezuela (MIZA) in Maracay, as required by the Venezuelan environmental authorities.

***Protopedaliodes ridouti* Viloría & Pyrcz,
new species
(Figs. 1, 7)**

Description. *Male.* Forewing length: 30 mm (n = 1). Eyes dark brown, hairy. Palpi twice as long as head, covered with long dark-brown hair. Antennae to over half costa. Thorax and abdomen all dark brown; walking legs (second pair) same length as in *P. kukenani* Viloría & Pyrcz (third pair broken in holotype). Forewing subtriangular, apex and tornus obtuse, outer margin convex and smooth; hindwing oval, outer margin smooth. Upperside all dark brown, blackish in basal and postbasal areas; faint, barely visible ocellus in cell M1, black with white pupil. Underside forewing ground color dark brown, sparsely sprinkled with lighter brown or silvery scales on apex and upper one third of submarginal area; ocellus in cell M1 large, as wide as cell, black, pupilled with white, circled with faint orange framing. Hindwing ground color similar to forewing but liberally sprinkled with lighter brown scales over the entire surface; lighter area between postmedian and submarginal lines, forming a 5–8 mm wide band, being the narrowest in cell M2 and towards tornus on vein 1A (3 mm), its inner and outer edge do not merge; two large ocelli in cells R5 and Cu1, of same shape, color and size as on forewing. Genitalia illustrated in Fig. 7.

Female. So far unknown.

Types. *Holotype.* Male, Mt. Roraima, 8000 ft, Venezuela, 12-ix-1974, B. V. Ridout, B. M. 1974-650, BM(NH) Rhopalocera vial number 4198.

Etymology. We dedicate the name of this species to its collector, Dr. B. V. Ridout.

Distribution. This species is only known from the summit of the Roraima-Tepui (=Mount Roraima, Fig. 11), where it probably flies sympatrically with *Protopedaliodes kukenani*, and another pronophiline species (presumably of the genus *Lymanopoda* Westwood; Orellana, pers. comm.). For a description of the habitats, vegetation, and general geographic aspects of this region, see Brewer (1984).

***Protopedaliodes profauna* Viloría & Pyrcz,
new species
(Figs. 2, 3, 8)**

Description. *Male.* Forewing length: 32–32.5 mm, mean = 32.25 (n = 2). Eyes coffee brown, covered by short black hairs. Palpi twice as long as head, pale brown; outer ventral long hairs coffee brown, inner hairs shorter and light brown. Antennae reaching half of costa, black, except for ventral region of club, which is brown. Body dorsally coffee brown with very shiny hairs, ventrally pale brown, lighter towards abdomen, in general very hairy (including leg femorae), but hairs denser and shorter than on dorsal surface. Forewing triangular, apex and tornus slightly rounded, outer margin slightly convex; hindwing subtriangular, tornus somewhat truncated, outer margin moderately scalloped. Dorsal ground color of wings

dark coffee brown, very shiny; creamy-light brown scales between veins in fringes of both wings; brownish sheen on hindwing anal margin region; forewing exhibiting very thick androconial patches in discal region; hindwing very hairy on basal two thirds. Underside ground color of wings similar to upperside; lighter postdiscal bands on both wings, laterally limited (except near tornus) by darkening of ground color. Forewing band anteriorly broadened, dusted with reddish scales; sparse white scales on subapical and apical regions, more densely in inner border of band near costa; sparse short white hairs along costal region. Hindwing covered by short creamy-white setae, more densely towards basal region, anal margin, and on discal band; reddish scales dusted over basal region, in space anterior to cell. Genitalia in Fig. 8.

Female. Forewing length: 33.5 mm (n = 1). The only known female is worn and differs from male in the following features: general color much paler; dorsal wing color rather paler towards distal third, particularly on forewing.

Types. *Holotype.* Male, Auyán-Tepui, 1700 m, Bolívar, Venezuela, 5°58'N, 62°32'W, 14/19-ii-1994, J. L. García, A. Chacón. *Paratypes.* 1 male same data; 1 female, Auyán-Tepui, 1800 m, Bolívar, Venezuela, 5°51'N, 62°35'W, 4/10-ii-1988, L. J. Joly & A. Chacón.

Etymology. This butterfly bears the name of one of the Venezuelan environmental institutions mentioned in the introduction. We do that because of the resulting euphony.

Distribution. Apparently endemic to the Auyán-Tepui (Fig. 11), an extensive table mountain massif in southeastern Venezuela. General accounts of the geography and ecological aspects of this region were presented by Brewer (1978) and Fundación Terramar (1993). *P. profauna* seems to fly in a different altitudinal zone located above the species described below.

***Pedaliodes terramaris* Viloría & Pyrcz,
new species
(Figs. 4, 9)**

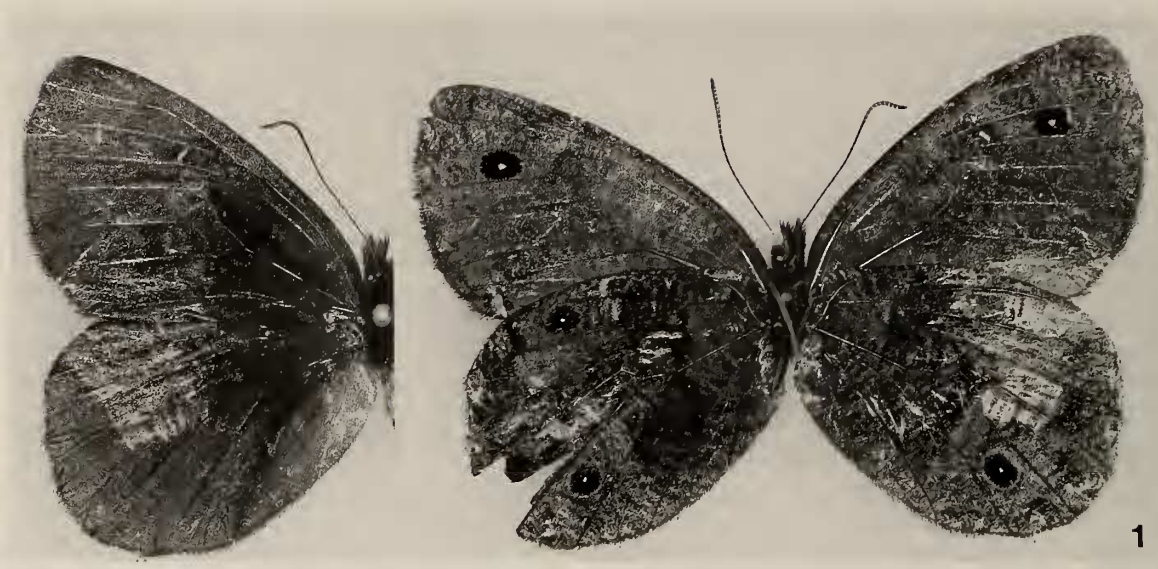
Description. *Male.* Forewing length: 27 mm (n = 1). Eyes black, covered by short black hairs. Palpi twice as long as head, hairy, dorsally and ventrally black, laterally creamy-white. Body dorsally covered by dark, bright, brown hairs, ventrally pale brown (including hairs covering femorae), somewhat reddish on anterior part of thorax. Forewing triangular, apex and tornus softly rounded, outer margin more or less linear; hindwing suboval, outer margin excavated between veins. Wing upperside ground color chocolate brown, very dark in discal region (of both wings), lighter towards basal region and distal third, except in marginal region; hindwing also lighter in marginal region. Forewing upperside bearing six androconial patches in discal region, the two elongated ones in cell Cu2 not as distant as in *P. yutajeana*, new species. Wing underside groundcolor chocolate brown, postdiscal bands lighter, bordered distinctly but irregularly with darker lines that never reach tornus; marginal region reddish chestnut, flanked by fine dark chocolate brown lines on both sides; forewing basal third, region adjacent to costa, and inner margin, almost as light as postdiscal band; basal half of wing densely covered by short brownish hairs; some white scales over costal portion of band inner border; discal cell finely sprinkled with dark chocolate brown scales. Hindwing underside sprinkled with brown and reddish scales (the latter less conspicuous on postdiscal band), anal region suffused with brick-orange, and dusted with yellow scales; two submarginal white dots within band in cells Cu2 and M3, respectively; basal region very hairy. Genitalia illustrated in Fig. 9.

Female. So far unknown.

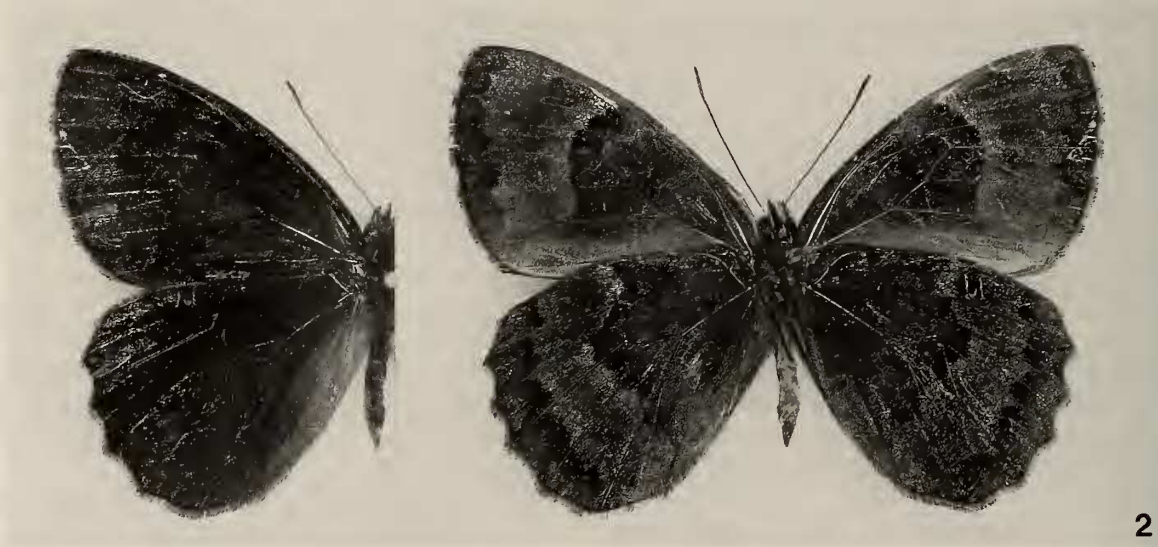
Types. *Holotype.* Male, Auyán-Tepui, 1500 m, Bolívar, Venezuela, 5°57'N, 62°39'W, 19/24-ii-1994, A. Chacón.

Etymology. The specific name, *terramaris*, is a derivation from the name of the Fundación Terramar, a private Venezuelan organization that has been responsible for much of the recent biological exploration of the tepuyes.

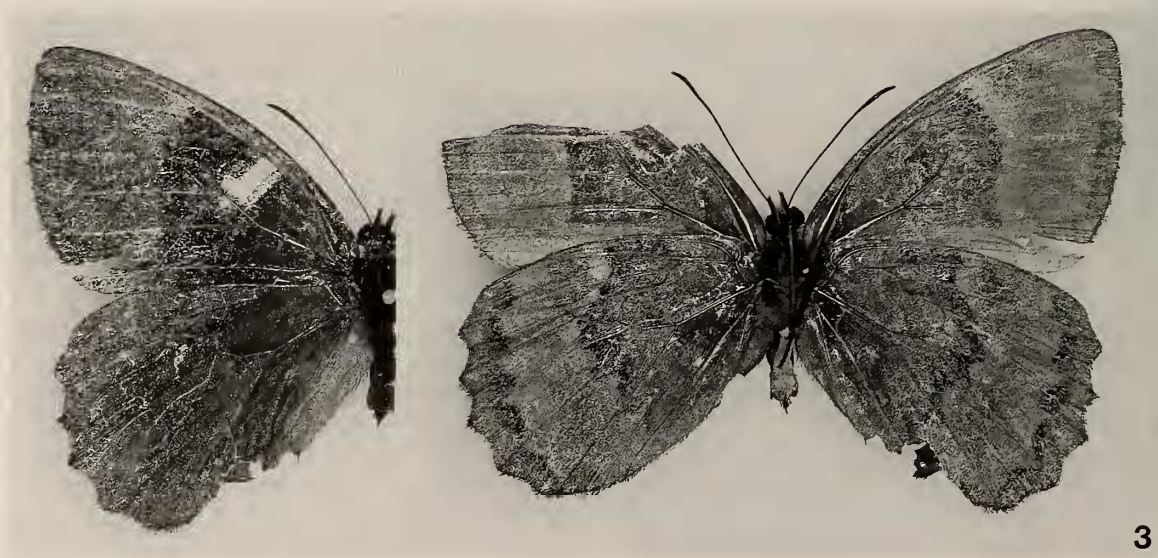
Distribution. Only known from the slopes of the Auyán-Tepui, where it flies in lower cloud forest.



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Pedaliodes yutajeana Viloría & Pyrcz,
new species
(Figs. 5, 6, 10)

Description. *Male.* Forewing length: 29 mm (n = 1). Eyes black covered by black hairs (with reddish sheen). Palpi twice as long as head, hairy, dorsally and ventrally black, laterally yellowish white. Antennae reaching approximately half of costa, dorsally dark brown, ventrally reddish. Thorax dorsally black, covered by very bright dark coffee hairs, as well as rest of body, ventrally lighter. Forewing triangular, apex and tornus slightly rounded, outer margin very softly sinuate; hindwing subtriangular, outer margin convex and moderately excavated between veins. Wing upperside ground color dark coffee brown, shiny, slightly lighter towards distal quarter (particularly in forewing), some light creamy-brown scales between veins in fringes; androconial patches on forewing discal region contiguous, two of them lengthened, and running parallel in cell Cu2. Wing underside ground color dark chocolate brown, lighter towards postmedial region. Forewing also lighter in basal quarter; some white scales dusted over costal region of band; reddish scales dusted over subapical region; six tiny submarginal white dots in cells R4 to Cu1; dense, short, reddish hairs on anterior portion of basal region. Hindwing postmedial band less distinct than on forewing; reddish suffusion in tornus and anal margin area; yellow scales dusted within band, from tornus along its inner margin, to costa; basal third of wing hairy; one submarginal white dot in cell Cu1, another one (vestigial) in M3; costal and marginal area with chestnut tone. Genitalia illustrated in Fig. 10.

Female. Forewing length: 30–32 mm, mean = 31 mm (n = 2). In general bigger than male, with less bright coloration. Dorsally with light postdiscal bands, which on hindwing containing a suffusion of brick-reddish in costal region near apex. Ventral pattern similar to male, but ground color with general speckling of reddish chestnut scales (almost imperceptible within bands); marginal region reddish; forewing submarginal white dots variable, sometimes missing; hindwing exhibiting a contrasting "marble pattern" as a result of reddish and chocolate brown speckling over plain brown ground color; yellowish scales uniformly dusted over entire surface, especially concentrated in inner border of postdiscal band; series of five submarginal white dots in cells R5 to A2; anal region with reddish suffusion as in male.

Types. *Holotype.* Male, Cerro Marahuaka, 2470 m, Parque Nacional Duida-Marahuaka, Amazonas, Venezuela, 3°37'N, 65°22'W, 3/6-ii-1992, Exp[edicación]. Terramar, J. Clavijo, A. Chacón. *Paratypes.* 1 female, Cerro Yutajé, 1750 m, Amazonas, Venezuela, 5°45'N, 65°08'W, 12/17-ii-1995, J. Clavijo A., Exp[edicación]. Terramar; 1 female, Cerro Yaví, 2200 m, Amazonas, Venezuela, 5°43'N, 65°54'W, 24/28-ii-1995, J. L. García, Exp[edicación]. Terramar.

Etymology. The name of the species is derived from one of the original localities, the Cerro Yutajé.

Distribution. This species is distributed in an extensive, discontinuous, montane area of northern Amazonas State, from Cerro Yaví and Yutajé to Cerro Marahuaka (Fig. 11). This range implies that it may also be found in the intervening mountains: the Sierra de Maigualida, Jaua-Sarisariñama massif, and certainly the Cerros Huachamacari and Duida, which are adjacent to the Marahuaka. Geographical and ecological aspects of the area, as well as recent biological discoveries, are discussed by Michelangeli et al. (1988) and Fundación Terramar (1989, 1993).

DISCUSSION

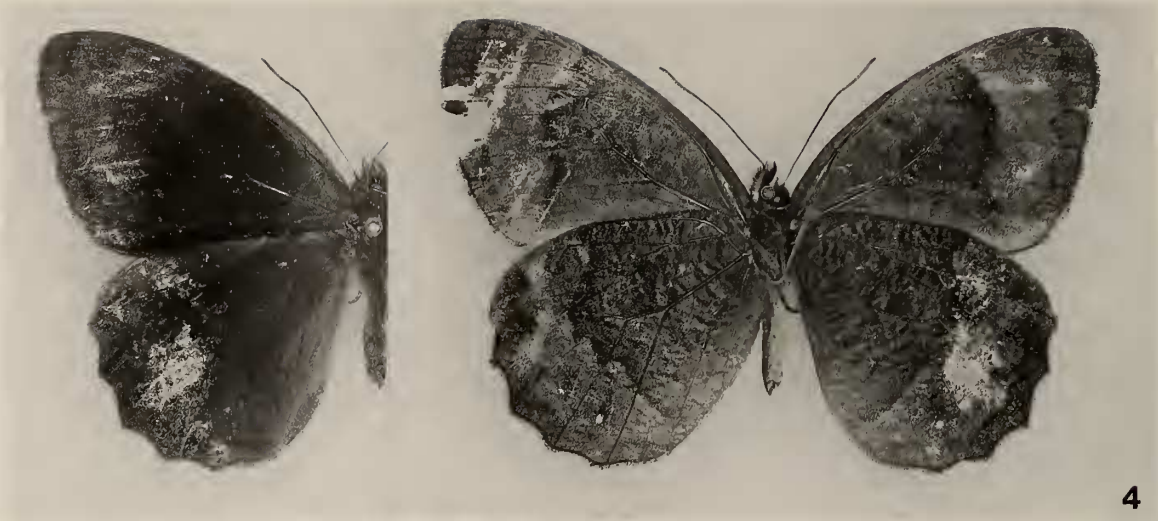
Protopedaliodes. The genus *Protopedaliodes* was recently erected for a species (*P. kukenani* Viloría & Pyrcz, 1994) from the upper cloud forest on neighboring table mountains in South-Eastern Venezuela, Kukenán-Tepui and Roraima-Tepui. Further research in 1995 in the Natural History Museum (BMNH) revealed the existence of a small collection of butterflies made by B. V. Ridout on the top of Mount Roraima. This material comprises 16 males and two females of *P. kukenani* (plus one male collected on the north ridge of Roraima, on the Guyana side, at 7400 ft., by Adrian Warren). This large series agrees with the original description of *P. kukenani* and no modifications of the specific diagnosis are required. However, among the Ridout material a single male was readily recognized to represent the second species of the genus (*P. ridouti*). In 1996 we examined the material recently collected on the tepuyes by staff members of the Museo del Instituto de Zoología Agrícola of the Universidad Central de Venezuela (MIZA), and found both *P. profauna* and the two species of *Pedaliodes* Butler also described in this paper. The above mentioned specimens of *Protopedaliodes*, plus the type series of *P. kukenani* (in MIZA) and five additional individuals of this species (three males, two females) obtained by the American mammalogist G. H. Tate in the summit of Roraima in 1927 (deposited in the American Museum of Natural History, New York [AMNH]), are to our knowledge the only ones existing in scientific collections.

Protopedaliodes ridouti is easily distinguished from its allies, *P. kukenani* and *P. profauna*, by its wing shape and quite different hindwing underside pattern, especially the well developed ocelli in cells R5 and Cu1. Although some specimens of *P. kukenani* also have faint ocelli in cell R5 of the underside of the forewing, in *P. ridouti* the ocelli are very well developed in forewing cell M1 and in cells R5 and Cu1 of the hindwing. The wing pattern of *P. ridouti* is unusual for pedaliidine butterflies, and is reminiscent, but perhaps not homologous to, that of the genus *Praepironophila* Forster (1964) (see also Miller 1986). It places *P. kukenani* well apart from other members of the tribe.

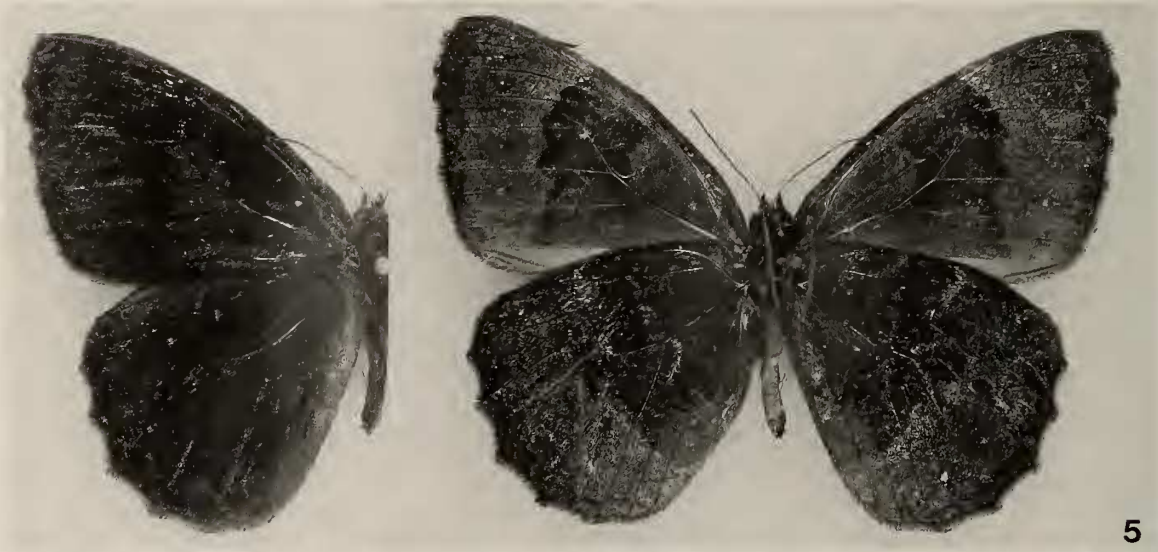
The type specimen of *P. ridouti* (30 mm) is slightly smaller than average sized *P. kukenani* (mean 32.8

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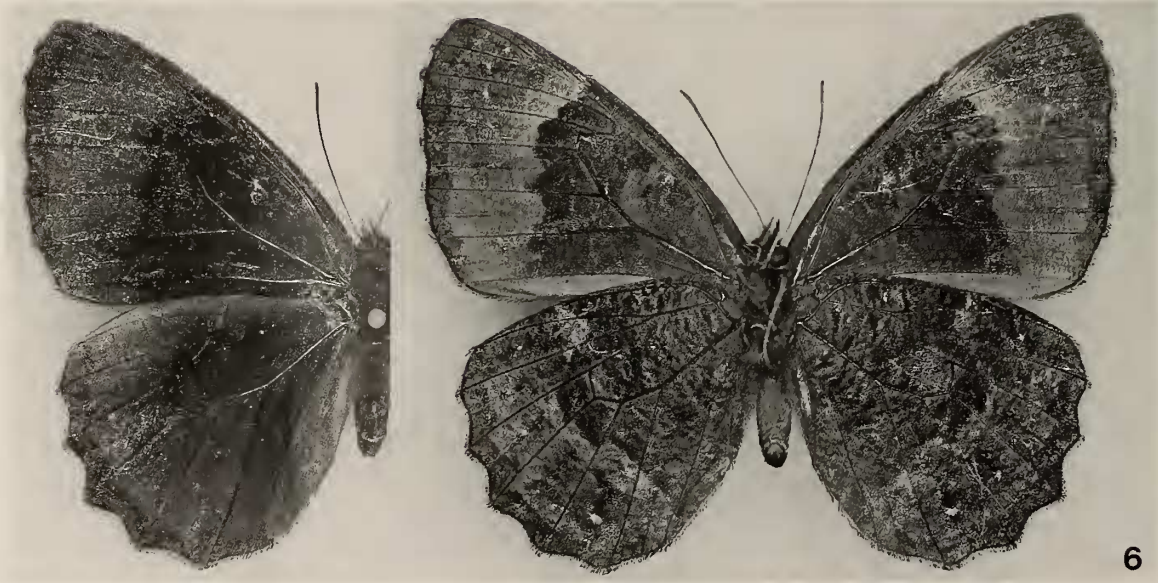
FIGS. 1–3. 1, *Protopedaliodes ridouti* Viloría & Pyrcz, new species, *Holotype*. Male, Mt. Roraima, 8000 ft, Venezuela, 12-ix-1974, B. V. Ridout. B. M. 1974-650, BM(NH) Rhopalocera vial number 4198; right upperside, left underside. 2, *P. profauna* Viloría & Pyrcz, new species, *Holotype*. Male, Auyán Tepui, 1700 m, Bolívar, Venezuela, 5°58'N, 62°32'W, 14/19-ii-1994, J. L. García, A. Chacón; right upperside, left underside. 3, *P. profauna* Viloría & Pyrcz, new species. Female paratype, Auyán Tepui, 1800 m, Bolívar, Venezuela, 5°51'N, 62°35'W, 4/10-ii-1988, L. J. Joly & A. Chacón; right upperside (forewing discal white mark represents rubbing of the scales), left underside.



4



5



6

mm). Its wing shape differs, the hindwing apical and tornal corner being more angular and giving the wings of *P. ridouti* a slightly square appearance. Venation is the same for all three species of *Protopedaliodes*, but the wing fringes of *P. ridouti* are shorter.

The male genitalia of *P. ridouti* show certain very characteristic features common to this species and to *P. kukenani*, such as the extremely long, straight and toothed aedeagus, and the deep saccus. On the other hand, subunci are nearly atrophied in *P. ridouti*, its uncus is even longer than in *P. kukenani*, and its valvae are devoid of any secondary process. The wing pattern of *P. profauna* is simple and resembles *P. kukenani*. The genitalia of *P. profauna* is structurally characteristic of the genus, but the aedeagus is three times as broad as those of the two other species, and it lacks the tooth at the tip; the uncus is relatively short, thickened, and remarkably bifurcated at the extremity (so far a unique feature in the tribe it belongs to, the Pronophilini); the saccus is as deep as in the two other species, although curved downwards; the valvae resemble those of *P. kukenani*, but are more stylized.

Common features among the species of *Protopedaliodes*, such as the ground color of the upperside, the lack of any androconial patch on the forewing upperside, similar head and leg morphology, and the characteristic male genitalia, confirm the validity of the genus when compared to other American Pronophilini.

The existence of further species of *Protopedaliodes* in the Guayana shield area (one certainly sympatric with *P. kukenani*) directly implies that some radiation occurred within the Pantepui which, until the present time, has been poorly researched, as compared to avian or mammalian faunas or high altitude floras. The cloud forest fauna of the upper slopes of the table mountains in the Pantepui seems to be impoverished compared to similar montane habitats in the Andes. This is possibly due to the isolation of this region and relatively small area of suitable cloud forest habitats. Most butterfly species (including *Pedaliodes*, see below) reported to date from the cloud forests of the Pantepui are endemic, but apparently offshots of the Andean fauna (see Strand 1912, Brown 1932, Viloría [1995], 1998, Viloría & Pyrcz 1995, Pyrcz 1995, Neild 1996), at least in those cases where affinities of the species can be recognized.

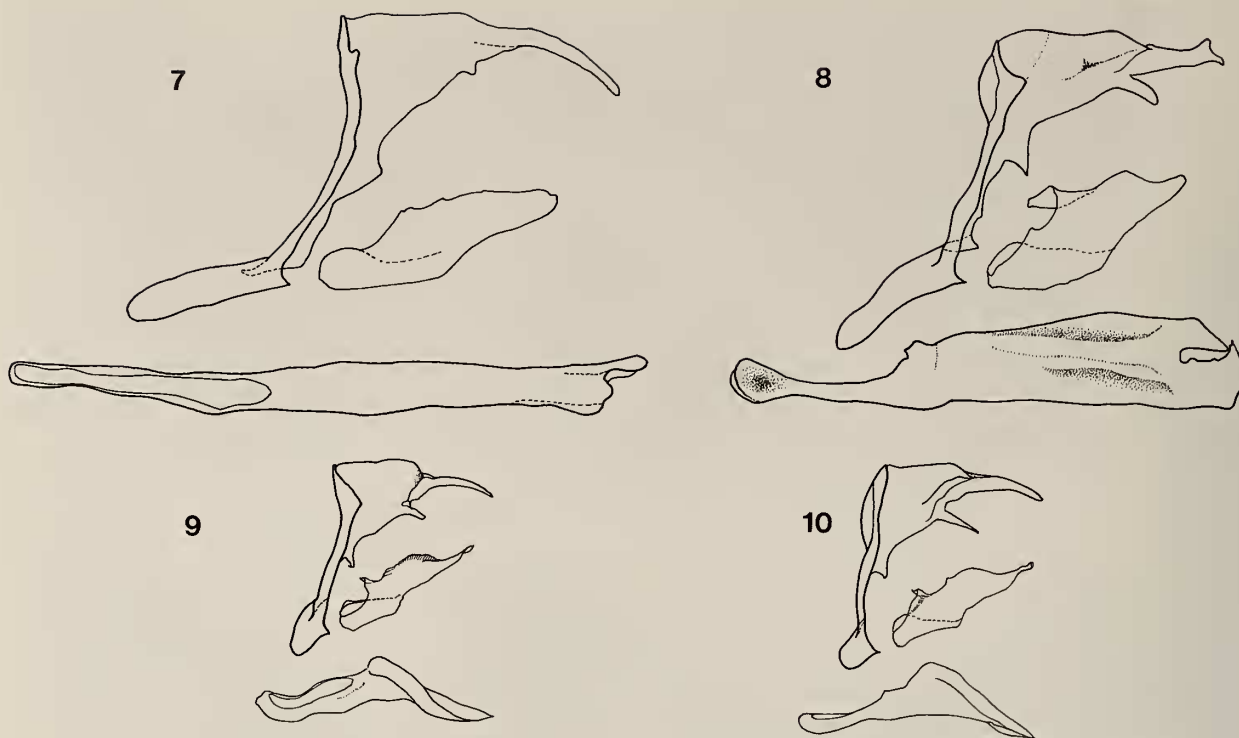
Protopedaliodes cannot yet be related with certainty to any pronophilines known from the Andes. We previously suggested that it has possible affinities with the less derived lineage of *Pedaliodes (sensu lato)* (i.e., *Praepronophila*, *Parapedaliodes* Forster). This assumption was based, among other characters, on male genitalic morphology (which is also reminiscent of that of *Praepronophila*).

It seems unlikely that *Protopedaliodes* originated from modern Andean "colonizers", and we favor the hypothesis that it is derived from older elements proper to the Pantepui. A fast adaptive radiation of *Protopedaliodes* could also be involved as a factor obscuring its phyletic origins.

Pedaliodes. *Pedaliodes* Butler *sensu stricto* is certainly one of the most speciose genera of Satyrinae in the world. We recognize 132 described valid species plus nine subspecies, and 105 species (excluding the two described here) plus 22 subspecies confidently identified as new, undescribed taxa, which are deposited in seven major entomological collections in America and Europe (Viloría unpubl.). This makes a grand total of 270 taxa, most of which are highly endemic to restricted montane areas of the tropical Andes. Only 15 species are known to occur out of the Andes, five of them being restricted to the mountains of the Pantepui (i.e., *P. roraimae* Strand, 1912 (Gran Sabana, Roraima-Tepui and Kukenán-Tepui, 1280–1900 m), *P. demarmelsi* Viloría, [1995] (Cerro de La Neblina, 1690–2100 m), *P. chaconi* Viloría, 1998 (Serranía de Tapirapecó, 1300 m), *P. terramaris* (Auyán-Tepui, 1500 m), and *P. yutajeana* (tepuyes of northern Amazonas State, from Cerro Yaví to Cerro Duida, 1750–2470 m)). Other alleged records from the Guayana region, such as *Pedaliodes prytanis* (Hewitson) (Adams & Bernard 1979:109) and *P. manis* (C. & R. Felder) (d'Abrera 1988:852), are incorrect. The first one is based on two old specimens mislabelled as being from Corosita, Caura Valley (in the BMNH), which were purchased by J. J. Joicey from Klages. This is obviously wrong as *P. prytanis* is endemic to the highest elevations of the Cordillera de La Costa, where Klages obtained part of his collections. The second case represents misidentifications of four males of *P. roraimae* (from Mount Roraima, Venezuela) in the same institution.

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FIGS. 4–6 4, *Pedaliodes terramaris* Viloría & Pyrcz, new species, *Holotype*. Male, Auyán Tepui, 1500 m, Bolívar, Venezuela, 5°57'N, 62°39'W, 19/24-ii-1994, A. Chacón; right upperside, left underside. 5, *P. yutajeana* Viloría & Pyrcz, new species, *Holotype*. Male, Cerro Marahuaka, 2470 m, Parque Nacional Duida-Marahuaka, Amazonas, Venezuela, 3°37'N, 65°22'W, 3/6-ii-1992, Exp. Terramar, J. Clavijo, A. Chacón; right upperside, left underside. 6, *P. yutajeana* Viloría & Pyrcz, new species, Female paratype, Cerro Yutajé, 1750 m, Amazonas, Venezuela, 5°45'N, 65°08'W, 12/17-ii-1995, J. Clavijo A., Exp. Terramar; right upperside, left underside.



FIGS. 7–10. Male genitalia of the species herein described; in each case aedeagus and left valva have been removed from natural positions. 7, *Protopedaliodes ridouti*. 8, *P. profauna*. 9, *Pedaliodes terramaris*. 10, *P. yutajeana*.

The species of *Pedaliodes* found south of the Orinoco River are all closely related, as deduced by the strong similarities in wing pattern and genitalia. With the exception of *P. demarmelsi* (which exhibits a very distinctive color pattern), they are, in fact, almost indistinguishable from each other in facies. *Pedaliodes terramaris* and *P. yutajeana*, however, can be told apart by subtle differences in size and wing shape (compare Figs. 4 and 5), and by the differences in the distribution of the male androconial patch on forewing cell Cu2 (see descriptions above). The shape and extent of the male forewing scent patches have proved to be most useful in identifying *Pedaliodes* species with few wing markings, and using these characters we have been able to recognize seven “black” species occurring sympatrically in the Colombian Cordillera Occidental (Pyrz & Vioria 1999b), all previously misidentified under one or two names (Adams 1986).

When compared, the valvae of *P. roraimae* and *P. chaconi* are shorter and more robust than those of *P. terramaris* and *P. yutajeana*. Differences between *P. roraimae* and *P. chaconi* were discussed in a previous publication (Vioria 1998).

The Pantepuian *Pedaliodes* belong to a group that is not restricted to the Guayana biogeographical region. On the contrary, this is the most widely distributed

clade within the genus, ranging from Mexico to Bolivia (see below). Vioria [1995] pointed out the structural and superficial similarities between the Pantepuian *P. demarmelsi*, and the Mesoamerican species *P. dejecta* (Bates) and *P. napaea* (Bates). This observation was at that time surprising, because of the apparently huge distributional gap between Mesoamerica and the Cerro de La Neblina, especially for these montane insects. However, a better understanding of the morphology, taxonomy, and distribution of a number of closely related species that occur at lower altitudinal levels (the lowest possible for the genus) in the cloud forest of almost every mountain range in between these range extremes has led us to believe that the group probably started diverging in isolation only geologically very recently, perhaps from a single widespread lowland ancestor.

Although Neotropical cloud forest satyrines are exceedingly sedentary and do not migrate (De Marmels et al. 1996, Vioria et al. in prep.), it is possible that past global climatic fluctuations may have led to the lowering and conjugation of cloud forests, enabling the ancestor of these butterflies to spread between currently isolated cloud forest “islands.”

Results of paleoclimatic studies in Venezuela (Rull 1996) and other areas of the northern Neotropics

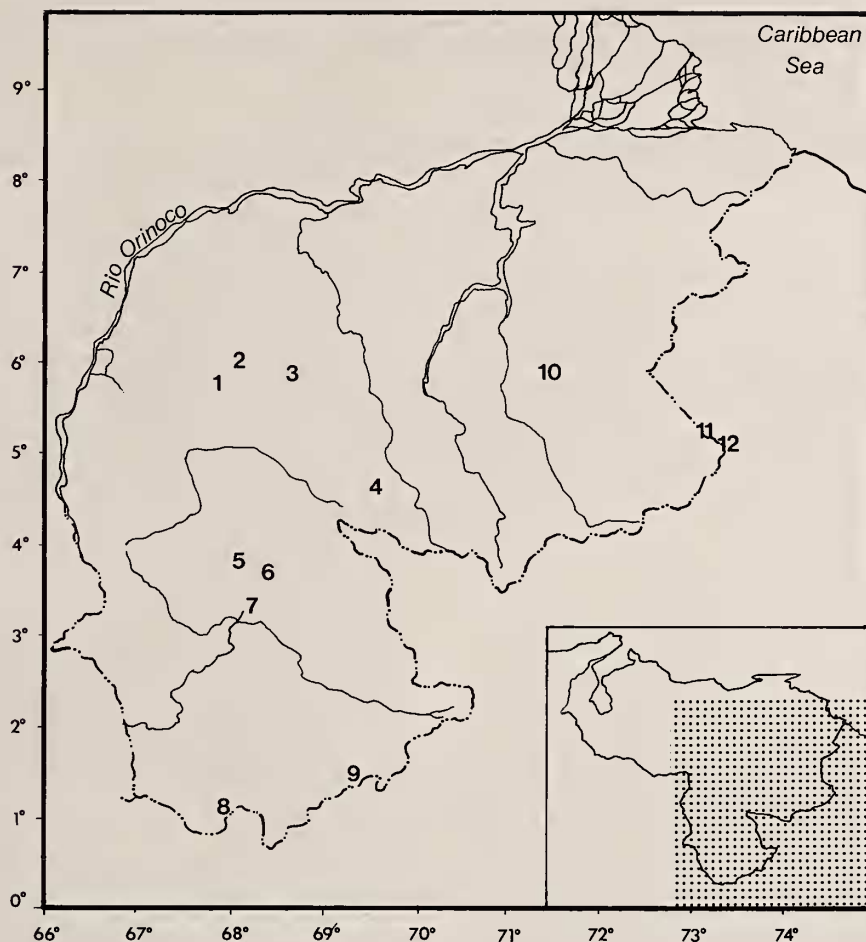


FIG. 11. Localities of the Pantepui region mentioned in the text: 1, Cerro Yutajé. 2, Cerro Yaví. 3, Sierra de Maigualida. 4, Jaua-Sarisariñama massif. 5, Cerro Huachamacari. 6, Cerro Marahuaka. 7, Cerro Duida. 8, Cerro de La Neblina. 9, Serranía de Tapirapécó. 10, Auyán-Tepui. 11, Kunenán-Tepui. 12, Roraima-Tepui (modified from Steyermark 1986, Fundación Terramar 1993 and Huber 1995).

(Schubert 1987), indicate much lower average temperatures at the end of the Pleistocene, and although conditions were also much drier in some areas, this does not rule out the possibility that the floristic equivalent of cloud forest could have been present in others. We speculate that not only the Pantepuiian *Pedaliodes*, but also all allied congeners¹ elsewhere in the Neotropics, may be derived from an ancestor which was widespread at lower elevations during the Pleistocene.

¹ The members of this group of allied congeners outside the Pantepui are: *Pedaliodes croizatorum*. Viloría and Camacho (Serranía del Turimikire, northeastern Venezuela, 1500–2300 m); *P. pisonia* (Hewitson) (Venezuelan Cordillera de La Costa, 1100–1700 m); *P. manneja* Thieme (Cordillera de La Costa and Sierra de Perijá, 1800–2300 m); *P. montagna* Adams & Bernard (Andes from Venezuelan Cordillera de Mérida to Bolivian Yungas, 1050–3000 m); *P. eretiba* (C. & R. Felder) (Cordillera Oriental, Colombia, ca. 1800 m); *Pedaliodes canela* (= *Pedaliodes canela*) Pyrcz and Viloría (Cordillera Occidental, Colombia, 1000–3300 m); *P. phrasiclea* Grose-Smith (Andes of Colombia to Bolivia, 1000–2250 m); *P. pomponia* (Hewitson) (Andes of southeastern Ecuador, 450–1400 m); *Pedaliodes balnearia* Pyrcz and Viloría (1999a)

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(southeastern Ecuador, 2000–2600 m); *Pedaliodes*, new species (Zamora valley, 1000–1300 m); *Pedaliodes*, new species, Lamas & Viloría, MS (southern Ecuador to northern Bolivia, 1800–2300 m); *P. phrasis* Grose-Smith (Andes of southern Peru and Bolivia, 750–3000 m); *P. prosa* Staudinger (southeastern Peru and Bolivia, 1000–3000 m); *P. dejecta* Bates (mountains of Panama, Costa Rica and Guatemala, 850–2300 m); *P. cremera* Godman & Salvin (Irazú volcano, Costa Rica, ca. 2000 m); *P. napaea* Bates (mountains of Guatemala and southern Mexico [Chiapas], 1000–1700 m); *P. circumducta* Thieme (Mexico, 1100–1450 m); *Pedaliodes* sp. [nov.] Luis-Martínez and Llorente (1993) (Mexico, Puerto Los Mazos, Jalisco, Michoacán Mountains and Sierra de Atoyac in Guerrero, ca. 1000–2000 m).

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